Research Article Journal of Orthoptera Research 2020, 29(1): 35-39

Mating behavior of the Persian boxer mantid, *Holaptilon brevipugilis* (Mantodea: Mantidae)

Mahmood Kolnegari[1]

1 Department of Entomology, Islamic Azad University of Arak, Markazi Province, Iran.

Corresponding author: *Mahmood Kolnegari* (mahkolnegari@yahoo.com)

Academic editor: *Matan Shelomi* | Received 21 June 2019 | Accepted 7 July 2019 | Published 13 March 2020

http://zoobank.org/5F48711C-1B2D-421F-826E-C07AE90CB62D

Citation: Kolnegari M (2020) Mating behavior of the Persian boxer mantid, *Holaptilon brevipugilis* (Mantodea: Mantidae). Journal of Orthoptera Research 29(1): 35–39. https://doi.org/10.3897/jor.29.37595

Abstract

The Persian boxer mantid, *Holaptilon brevipugilis*, is the mantid most recently described from Iran. Here, I present some aspects of the courtship display and mating behavior of this species. I conducted 28 mating trials, quantified the relative frequency of all mating behaviors, and estimated the pre-copulation, copulation, and post-copulation periods. I also compared the effects of frontal vs. lateral approaches of the male for mating success, since frontal approach increases the risk that the male will be seen and cannibalized by the female. In 64% of trials, the male approached the female immediately, regardless of whether the female could see him or not. Copulation was successful in 61% of trials. Male courtship consisted of dorsoventral bending of the male's abdomen and occurred in 10% of all trials, but only when the female was facing the male. In contrast, trembling of the forelimbs was not associated with copulation, occurred in 10% of all trials, and was always followed by the male moving away from the female. I observed one female cannibalizing a male post-copulation. The Persian boxer mantid might be sexually cannibalistic, but confirming this hypothesis would require further studies, including a focus on female hunger level as a determining factor in sexual cannibalism and in male courtship behaviors.

Keywords

courtship, deimatic behavior, experiment, forelimb trembling, Iran, sexual cannibalism

Introduction

Descriptions of courtship displays and their prevalence are relatively rare for Mantodea (Battiston 2008). The mating behavior of mantids can be divided into two main categories: male-originated mating behavior, or courtship; and female-originated mating behavior, or sexual cannibalism. These two types are interconnected. A higher likelihood of sexual cannibalism can increase the rate of courtship and, consequently, courting decreases the probability of sexual cannibalism (Maxwell 1998, Lelito and Brown 2006, Barry et al. 2008b, Jayaweera et al. 2015, Kadoi et al. 2017). The structure of courtship and the frequency of sexual cannibalism were the subjects of a few research studies (Edmunds 1975, Loxton 1979, Liske and Davis 1987, Battiston 2008). Male-originated courtship often includes movement of body parts when approaching the female. Some of these courtship movements include "boxing" of the prothoracic legs by *Oxypilus hamatus* Roy (Edmunds 1975), "semaphore" and "stamping" with the metathoracic legs by *Ephestiasula amoena* (Bolivar) (Loxton 1979) and *Acontiothespis multicolor* (Saussure) (Quesnel 1967), "pumping" and "weaving" of the abdomen by *Tenodera aridifolia sinensis* (Saussure) (Liske and Davis 1987), and "trembling" by *Oligonyx insularis* Bonfils (Bonfils 1967). Female attacks on a male can occur before, during, and after copulation (Lelito and Brown 2006, Jayaweera et al. 2015). The frequency of sexual cannibalism differs from one species to another (Maxwell 1999) and can be affected by factors such as female hunger levels and the approach direction of the males (Maxwell 1998, Barry et al. 2008a).

In this study, I focused on courtship and sexual cannibalism in a recently described mantid species, *Holaptilon brevipugilis* Kolnegari, or the Persian boxer mantid. *H. brevipugilis* belongs to a rare genus, having just one identified congeneric species with a small distribution range (Beier 1964, Abu-Dannoun and Katbeh-Bader 2007, Kolnegari and Vafaei-shoushtari 2018). This wingless species, which was recently discovered in the center of Iran, is one of the smallest mantids in the world with a body size range of 1.2–1.6 cm (Roy 1999, Kolnegari and Vafaei-shoushtari 2018). The name of the species comes from the occasional trembling movement of its oversized grasping forelimbs. Such behavior was observed in both males and females, though it is apparently more frequent in males (Kolnegari and Vafaei-shoushtari 2018). The behavior was observed in the laboratory mostly during encounters with other individuals (different- or same-sex), and rarely arose before hunting prey (e.g., housefly). In addition, numerous males and females were observed performing characteristic forelimb movement during specimen collection from their wild habitat, but this behavior was not associated with escape from collectors nor encounters with other mantids or prey.

The main question of this study is whether foreleg trembling has a determinative function in the mating process of the mantid as a possible courtship display (Bonfils 1967, Edmunds 1975, Battiston 2008). Additional questions include whether or not, and how frequently, female-originated sexual cannibalism occurs in

boxer mantids. Elucidating the behavioral complexities of mating in this species could help to inform the systematic position and evolutionary history of this rare genus.

Materials and methods

I collected adult individuals of *Holaptilon brevipugilis* from their only known habitat around Arak City, Iran, during June-July 2017. I collected 28 males and 28 females and reared them on a diet of one small housefly (*Musca domestica*) three times a week. Animals were kept individually within well-ventilated, 30-cm-diameter opaque plastic containers in the laboratory, at a temperature of 20–22 °C. The same conditions were used for 28 staged mating trials that allowed an observation of general male mating behavior. I paid particular attention to behaviors such as courtship display, approach pattern, jumping distance, male mating success, and copulation duration.

Habitat structure, particularly the type of flora, can impact mating behavior based on the objects the mantids are situated on (Younes 2007, Battiston 2008). The boxer mantid in the wild resides in a stony habitat covered with low vegetation. Fortunately, I was able to easily rebuild this environment in the laboratory. Following Liske and Davis (1987), I illuminated the mating arena in an otherwise darkened room. This enabled me to observe the behaviors without disturbing or stressing the mantids. Since hungry females are more likely to cannibalize males than well-fed females (Liske and Davis 1987, Hurd et al. 1994, Kadoi et al. 2017), I provided a satiating diet for females. Experimental pairs were randomly chosen for copulation three hours after feeding; therefore, females were not hungry during the mating experiments. Pairs were excluded after each trial, so each pair was used only once.

Approximately 30 min after the initial introduction of a female, a male was placed into the container at least 20 cm away from the female. If an interaction did not occur within three hours, the trial was terminated. Alternatively, if courtship and copulation occurred, then the male approach conditions and duration of mating were recorded. I examined the effects of two orientations of encounter on courtship behavior according to previous studies (Lelito and Brown 2006, Barry et al. 2008b, Battiston 2008). The approach orientations were 'frontal', where males approached the female from the front and faced her within her visual field of not more than 80°, and 'lateral', where the male approached from completely outside the female's visual field towards the rear of the female. These were established by placing the male in the container either in front of or laterally and somewhat behind the female. For each approach orientation, 14 trials were carried out.

I used a Canon SX240HS digital camera to record all trials, and a professional camera, Canon 7D (Mark 2), to take high-resolution photos of any notable behaviors. The variables measured included the distance from the female at detection, how the male detected the female (based on signs of abundant antennal movements or visual fixation), male jumping distance, pre-copulation duration, copulation duration, and post-copulation duration. I also paid attention to possible courtship behaviors as previously reported from other mantodeans, such as lateral swaying, abdomen bending, and rhythmic movements of legs. Due to possible directional changes by the sexes during the encounters, I considered the resulting direction instead of initial direction for jumping. I recorded pre-copulatory mounting duration as the time from mounting to the genital linkage, copulation duration as the time from linkage to separation of the genitalia, and post-copulation duration as the time from the end of intromission until the male leaped off the female (according to Lelito and Brown 2006). I used multivariate ANOVA to analyze the data with SAS software (version 9.1). Mean and standard deviation were calculated with Microsoft Excel.

Results

Components of male sexual behavior typically included the following: oscillation of antennae, visual fixation on the female, quick running, cessation of movement, repeated downward and upward bending of the abdomen, and jumping on the female's back from 2.2±0.4 cm away. The dorsoventral rhythmic movement of the male's abdomen was typical of courtship and started slightly downward (plantar flexion), then continued with an upward variable bending (dorsiflexion) at an angle of 0° to 90° (Fig. 1). The male sexual behavior was comprised of three phases.

Phase 1: Male orientation.—The initial approach occurred when a male sensed a female and began abundant antennal movements and prolonged viewing of her. These behaviors occurred within 15±1.9 cm of the females with no significant difference between frontal and lateral male release ($F = 2.68$, $df = 1, 22$, $p = 0.4$). In five of the 28 trials (one frontal and four lateral), the males did not interact with the females within three hours; these were excluded from the dataset. Lateral swaying was not observed in any intersexual approaches during this experiment. Seventy-eight percent of males that noticed a female moved quickly toward the female. Sixty-seven percent of these moving males mounted without courtship. Twenty-two percent of males that noticed a female were motionless until the female began to advance. This behavior occurred more frequently in frontal encounters than lateral encounters (Fig. 2). Thirty-eight percent of initially frontal encounters changed to lateral encounters as males changed their approach route. Meanwhile, 20% of lateral encounters became frontal encounters because of female awareness and subsequently turning to face the male. Flexion of the abdomen and forelimb waving occurred only when males and females were facing each other. Regardless of initial approach, 21% of the trials (n = 6) resulted in face-face encounters, which led males to display one of these rhythmic movement. While abdomen bending was a typical form of courtship, forelimb waving was not followed by mounting in the study.

Among frontal encounters (n = 13), five males started to move then changed their orientation from frontal to lateral and stopped within 2.2±0.4 cm of females (i.e., "jumping distance"). Two males demonstrated flexion of the abdomen seven and eight times in 10 and 11 seconds, respectively, in what could be considered courtship behavior (Fig. 1), then reached the jumping point. Another two males responded to the female by trembling their forelimbs, displaying the patterned interior faces and waving them in slow arcs, before moving away from the female. Therefore, forelimb trembling did not seem to be a component of courtship. Four males did not move but waited for the female to approach to jumping distance.

Among lateral encounters (n = 10), one male did not move and waited for the female to approach to jumping distance. Nine males moved towards the females. Two of these moving males faced the females frontally because she changed her direction. One of these two males demonstrated flexion of abdomen (six times in 11 seconds) and reached the jumping point, the other male trembled his forelegs before moving away from the female who followed after him (Fig. 3). The seven remaining males reached jumping distance and did not show rhythmic movement.

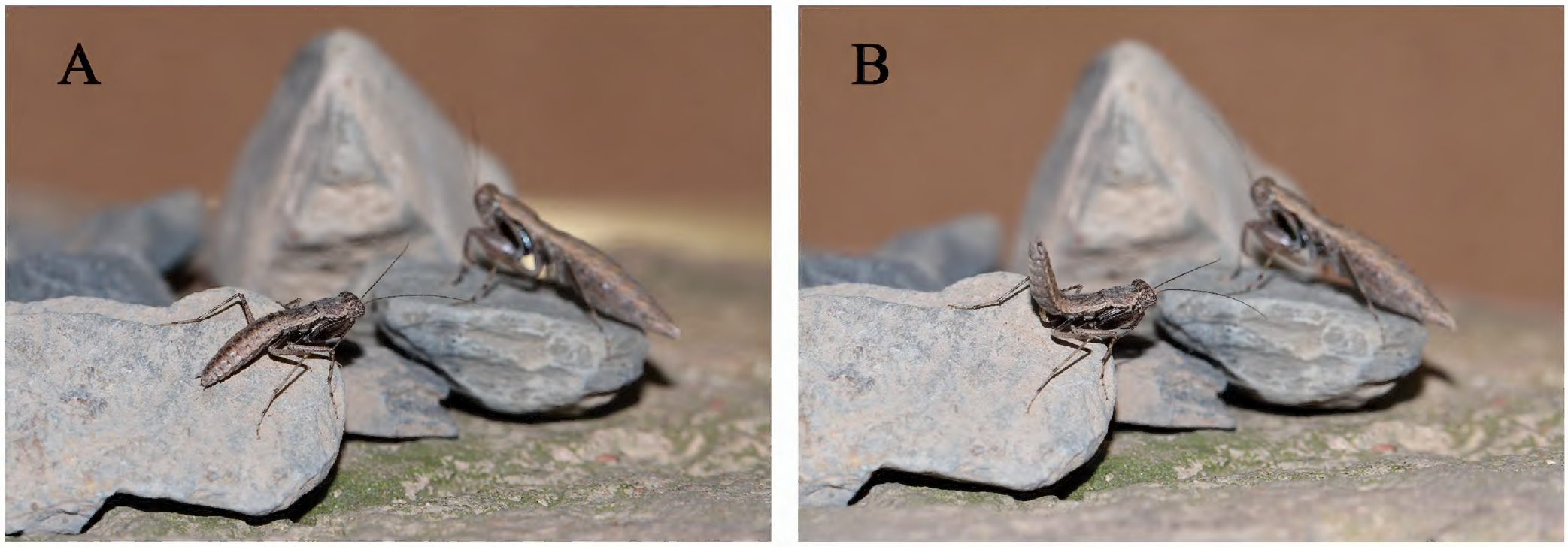

Fig. 1. Orientation of male *Holaptilon brevipugilis* abdomen in a frontal encounter with a female prior to copulation. **A.** Plantar flexion and **B.** Dorsiflexion of the abdomen. The male is in the foreground on the left and the female is to the rear and to the right of the male.

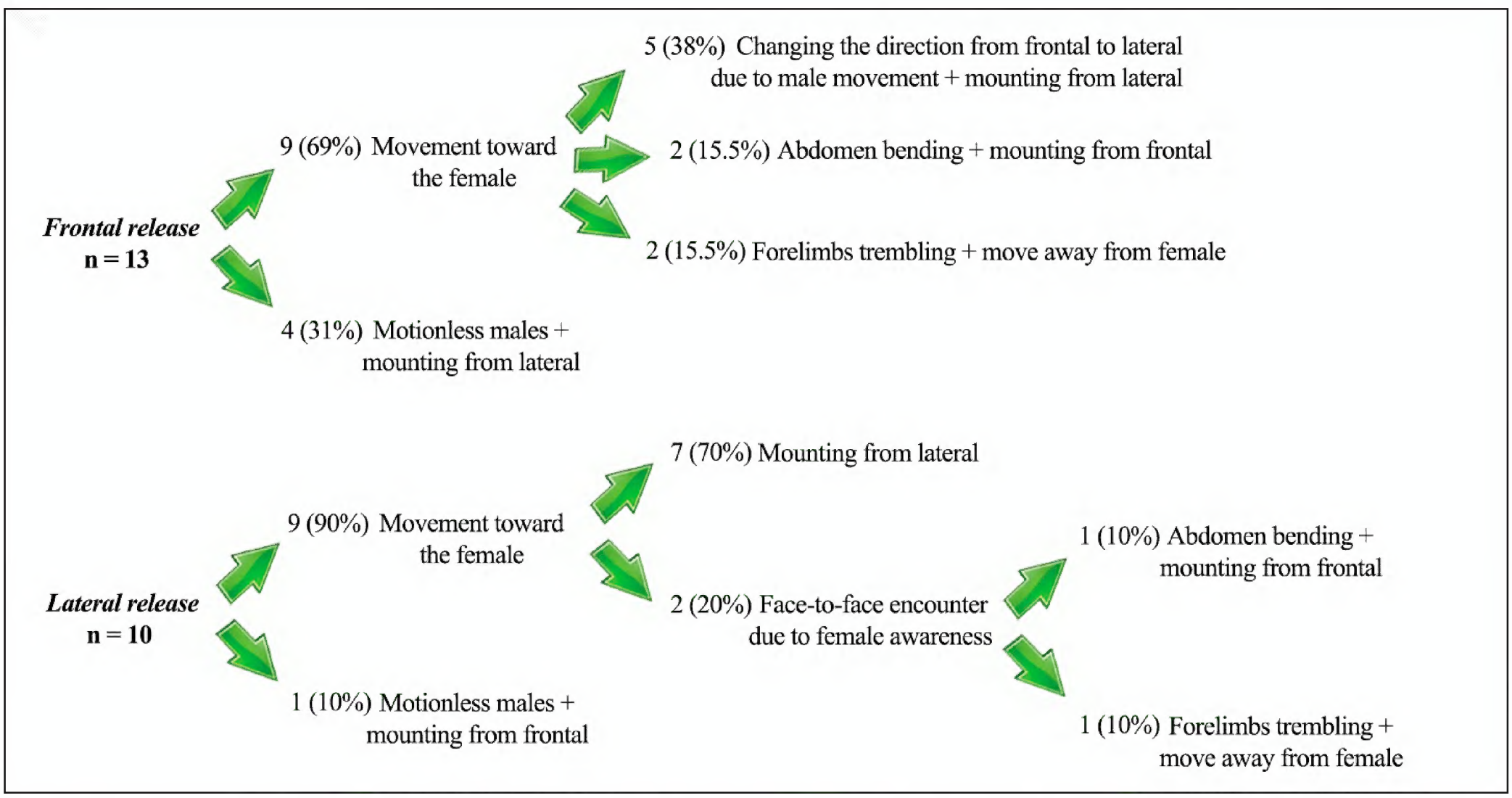
Frontal release
n = 13
9 (69%) Movement toward the female
5 (38%) Changing the direction from frontal to lateral due to male movement + mounting from lateral
2 (15.5%) Abdomen bending + mounting from frontal
2 (15.5%) Forelimbs trembling + move away from female
4 (31%) Motionless males + mounting from lateral
Lateral release
n = 10
9 (90%) Movement toward the female
7 (70%) Mounting from lateral
2 (20%) Face-to-face encounter due to female awareness
1 (10%) Abdomen bending + mounting from frontal
1 (10%) Forelimbs trembling + move away from female
1 (10%) Motionless males + mounting from frontal

Fig. 2. The sequence of mating behavior of *Holaptilon brevipugilis* showing the number and the percentage of males at each stage. One frontal encounter and four lateral encounters did not lead to any interaction between males and females, so they were excluded from the dataset.

Phase 2: Male mounting.—This phase was characterized by males jumping onto the female for copulation (mounting) from a distance of 2.2±0.4 cm from the female. Nine males that initially encountered females laterally and eleven males that initially encountered females from a frontal position entered the mounting phase. Sixty percent of these males mounted the female from a lateral position and 40% mounted from a frontal (face-to-face) position. Almost all males leaped successfully, with just one male with a frontal orientation miscalculating the distance and lying under the female after jumping (Fig. 4A). The orientation prior to the jump had a significant effect on jumping distance ($F = 8.43$, $df = 1, 19$, $p = .017$), so males mounting from a frontal position leapt from greater distances than males mounting females from a lateral position.

Phase 3: Copulation.—As soon as the male mounted the female, he began the characteristic, approximately 45° angle S-bending mating movements of his abdomen similar to those described for *Tenodera aridifolia sinensis* (Liske and Davis 1987, Lelito and Brown 2006). There was an interesting bias in abdomen S-bending direction not mentioned in prior literature, as males preferred to bend the abdomen from the left side in 95% of trials (Fig. 4B).

Fig. 3. Trembling and showing the shiny colored surface of forefemora by a *Holaptilon brevipugilis* male during a frontal encounter with a female.

Fig. 4. Copulation behavior in *Holaptilon brevipugilis.* **A.** Male mounting failure. Male is underneath the female. **B.** Copulation. Smaller male is on top of the larger female.

Sixteen of the 28 trials led to copulations that occurred 5–28 seconds after mounting. One trial in which the male mounted in a reverse position delayed this pre-copulation period for more than four minutes. I terminated two trials after males mounted for 20–24 minutes but did not successfully contact the female's genitalia. Body measurement confirmed those two males (with 1.05 and 1.07 cm body length) were among the smallest males, while those two females (with 1.77 and 1.86 cm body length) were larger than the average female (1.6 cm body length).

Copulation lasted 5.76±1.06 hours and post-copulation duration was 9.88±1.4 minutes. Neither copulation duration nor post-copulation duration differed significantly between frontal and lateral encounters ($F = 44.2$, $df = 1, 17$, $p = 0.71$ and $F = 9.6$, $df = 1, 17$, $P = 0.26$).

I recorded just one case of cannibalism, which occurred after mating when a male separated from the female.

Discussion

The male mantid presents a complicated series of mating behaviors, which can differ between species. These behaviors induce behavioral isolation as a barrier to mating with other species (reviewed in Gray 2005). Adult male Persian boxer mantids in this study performed a rather simple mating pattern that included moving closer to the female and leaping onto her back from a conserved distance. Males most frequently mounted females from a lateral approach, consistent with the idea that males try to reduce the probability that they will be cannibalized during intersexual encounters by avoiding the visual field of females (Liske and Davis 1987, Maxwell 1998). However, in face-to-face encounters, males lifted and bent their abdomens, which may be a form of courtship. Male courtship frequency was inconsistent, which we would expect if males adjust their behaviors in ways that minimize the chance of being attacked (Jayaweera et al. 2015).

In this study, female *H. brevipugilis* rarely performed sexual cannibalism, though future studies could examine the effect of female hunger level on this behavior. *H. brevipugilis* nymphs did not have any cannibalistic activity (personal observation), and so it is possible that *H. brevipugilis* is an infrequently cannibalistic mantid. On the other hand, hungry females might not be able to easily consume males during copulation because of considerable sexual dimorphism, although this conclusion needs further investigation.

Orientation of approach had a significant effect on the Persian boxer mantid males' jumping distance, while Lelito and Brown (2006) found that factor did not have a significant effect on Chinese mantid (*Tenodera aridifolia sinensis* (Saussure)) male jumping distance. Increased male jumping distance decreases the likelihood of cannibalism (Lelito and Brown 2006), so future studies

on Persian boxer mantid should investigate the correlation of female hunger levels to male jumping distance. However, both the frequency of female-on-male cannibalism and the jumping distance of males in the Persian boxer mantid could be dependent on female hunger level and changeable under different conditions.

I did not identify when and why males and females of Persian boxer mantids performed foreleg trembling, but I concluded that this is not related to mating behavior because males that displayed this behavior tended to move away from the female rather than mating with her. However, forelimb trembling could demonstrate threat posture, which has been known as "deimatic behavior" in mantodeans (Maldonado 1970, Umbers et al. 2015) and could explain why this behavior was observed when specimens were being field collected. By contrast, males of *Ephestiasula amoena* (Bolivar) move their forelimbs to expose a bright pattern on the inside face of the expanded, plate-like forefemora before mating (Loxton 1979). Flexion of the abdomen, another rhythmic movement of Persian boxer mantid, is more likely associated with mating. Bending of the abdomen in *H. brevipugilis* follows a different pattern from *Hestiasula major* (Beier), which moves the abdomen laterally (personal observation). Additionally, the Persian boxer mantid male starts this rhythmic motion with a slightly downward movement (Fig. 1A), unlike *Pseudomantis albofimbriata* (Barry et al. 2008b) and *Tenodera sinensis* (Liske and Davis 1987) that show only upward abdomen bending.

I did not observe any lateral swaying or side-to-side movement in the boxer mantid, while this behavior is a component of *Pseudomantis albofimbriata* males' sexual behavior (Barry et al. 2008b). The Persian boxer mantid's flexion of the abdomen only occurred in some frontal encounters; however, Lelito and Brown (2006) observed this behavior in lateral encounters of *Tenodera aridifolia sinensis*, although they provided evidence that frontal encounters induced Chinese mantid males to bend their abdomens with a greater angle. In fact, both above-mentioned studies showed that frontal encounters increase the degree of the male's movements.

In a broader context, courtship display has some correlations with taxonomic categories. "Abdomen movement" has been observed in all four studied species in the Mantidae family (*Holaptilon brevipugilis*, *Tenodera aridifolia*, *Ameles decolor*, *Pseudomantis albofimbriata*) and only one third of the studied species in the Hymenopodidae family (*Hestiasula major*) (Liske and Davis 1987, Barry et al. 2008b, Battiston 2008). The similarity of courtship behavior in such taxonomically distant species of praying mantids may suggest this behavior is quite old, and could have been present in a common ancestor. Of course this might also be explained as convergence, but using the same structures to signal in the same way would seem an improbable result of separate evolution (Battiston 2008). Though we now know the courtship displays of the Persian boxer mantid, we need to study such behaviors in other members of the Mantidae in general and, more specifically, the Amelinae subfamily, to understand their evolutionary history.

Acknowledgements

I would like to thank Dr. Matan Shelomi and Dr. Saeed Alaei for English improvement of the manuscript, as well as Ms. Mandana Hazrati and Mr. Reza Babaei-pour for their help in the field survey and laboratory trials.

References

Abu-Dannoun O, Katbeh-Bader A (2007) Mantodea of Jordan. Zootaxa 1617: 43–56. https://doi.org/10.11646/zootaxa.1617.1.2

Barry KL, Holwell GI, Herberstein ME (2008a) Female praying mantids use sexual cannibalism as a foraging strategy to increase fecundity. Behavioural Ecology 19: 710–715. https://doi.org/10.1093/beheco/arm156

Barry KL, Holwell GI, Herberstein ME (2008b) Male mating behaviour reduces the risk of sexual cannibalism in an Australian praying mantid. Journal of Ethology 27: 377–383. https://doi.org/10.1007/s10164-008-0130-z

Battiston R (2008) Mating behaviour of the mantid *Ameles decolor* (Insecta, Mantodea): Courtship and cannibalism. Journal of Orthoptera Research 17: 29–33. https://doi.org/10.1665/1082-6467(2008)17[29:MBOTMA]2.0.CO;2

Beier M (1964) Ein neues mantiden-genus aus Israel. Israel Journal of Zoology 13: 184–186.

Bonfils J (1967) Contribution à l'etude des orthoptéroides des Antilles 111. Une espece nouvell dugenre *Oligonyx* Saussure: description et notes biologiques (digt.). Bulletin de la Société Entomologique de France 72: 243–248.

Edmunds M (1975) Courtship, mating, and possible sex pheromones in three species of Mantodea. Entomologist's Monthly Magazine 111: 53–57.

Gray DA (2005) Does courtship behaviour contribute to species-level reproductive isolation in field crickets? Behavioural Ecology 16: 201–206. https://doi.org/10.1093/beheco/arh144

Hurd LE, Eisenberg RM, Fagan WF, Tilmon KJ, Snyder WE, Vandersall KS, Datz SG, Welch JD (1994) Cannibalism reverses male-biased sex ratio in adult mantids: female strategy against food limitation? Oikos 69: 193–198. https://doi.org/10.2307/3546137

Jayaweera A, Rathnayake DN, Davis KS, Barry KL (2015) The risk of sexual cannibalism and its effect on male approach and mating behaviour in a praying mantid. Animal Behaviour 110: 113–119. https://doi.org/10.1016/j.anbehav.2015.09.021

Kadoi M, Morimoto K, Takami Y, Ethol J (2017) Male mate choice in a sexually cannibalistic species: Male escapes from hungry females in the praying mantid *Tenodera angustipennis*. Journal of Ethology 37: 177–185. https://doi.org/10.1007/s10164-017-0506-z

Kolnegari M, Vafaei-shoushtari R (2018) The first Persian boxer mantid, a new species of *Holaptilon* Beier, 1964 from Haftad-gholeh Protected Area, Iran (Mantodea, Mantidae). Journal of Entomological Research 10: 9–17.

Lelito JP, Brown WD (2006) Complicity or conflict over sexual cannibalism? Male risk taking in the praying mantis *Tenodera aridifolia sinensis*. The American Naturalist 168: 263–269. https://doi.org/10.1086/505757

Liske E, Davis WJ (1987) Courtship and mating behaviour of the Chinese praying mantis, *Tenodera aridifolia sinensis*. Animal Behaviour 35: 1524–1537. https://doi.org/10.1016/S0003-3472(87)80024-6

Loxton RG (1979) On display behaviour and courtship in the praying mantis *Ephestiasula amoena* (Bolivar). Zoological Journal of the Linnean Society 65: 103–110. https://doi.org/10.1111/j.1096-3642.1979.tb01083.x

Maldonado H (1970) The deimatic reaction in the praying mantis *Stagmatoptera biocellata*. Zeitschrift für vergleichende Physiologie 68: 60–71. https://doi.org/10.1007/BF00297812

Maxwell MR (1998) Lifetime mating opportunities and male mating behaviour in sexually cannibalistic praying mantids. Animal Behaviour 55: 1011–1028. https://doi.org/10.1006/anbe.1997.0671

Maxwell MR (1999) Mating behavior. In: Prete FR, Wells H, Wells PH, Hurd LE (Eds) The Praying Mantids. Johns Hopkins University Press, Baltimore, 62–99.

Quesnel VC (1967) Observations on the reproductive behaviour of the mantis *Acontiothespis multicolor*. Journal Trinidad and Tobago Field Naturalist's Club 1967: 53–56.

Roy R (1999) Morphology and Taxonomy. In: Prete FR, Wells H, Wells PH, Hurd LE (Eds) The Praying Mantids. Johns Hopkins University Press, Baltimore, 19–41.

Umbers KDL, Lehtonen J, Mappes J (2015) Deimatic displays. Current Biology 25: 58–59. https://doi.org/10.1016/j.cub.2014.11.011

Younes A (2007) Laboratory study of cannibalism in *Sphodromantis viridis* Forskal (Mantodea: Mantidae): Effects of prey availability, habitat structure, and predator density. Egyptian Journal of Pest Control 17: 57–63.